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ORIGINAL RESEARCH

Intraspecific alternative phenotypes contribute to variation in species' strategies for growth

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Abstract

Ecologists have historically sought to identify the mechanisms underlying the maintenance of local species diversity. High-dimensional trait-based relationships, such as alternative phenotypes, have been hypothesized as important for maintaining species diversity such that phenotypically dissimilar individuals compete less for resources but have similar performance in a given environment. The presence of alternative phenotypes has primarily been investigated at the community level, despite the importance of intraspecific variation to diversity maintenance. The aims of this research are to (1) determine the presence or absence of intraspecific alternative phenotypes in three species of tropical tree seedlings, (2) investigate if these different species use the same alternative phenotypes for growth success, and (3) evaluate how findings align with species co-occurrence patterns. We model species-specific relative growth rate with individual-level measurements of leaf mass per area (LMA) and root mass fraction (RMF), environmental data, and their interactions. We find that two of the three species have intraspecific alternative phenotypes, with individuals within species having different functional forms leading to similar growth. Interestingly, individuals within these species use the same trait combinations, high LMA × low RMF and low LMA × high RMF, in high soil nutrient environments to acquire resources for higher growth. This similarity among species in intraspecific alternative phenotypes and variables that contribute most to growth may lead to their negative spatial co-occurrence. Overall, we find that multiple traits or interactions between traits and the environment drive species-specific strategies for growth, but that individuals within species leverage this multi-dimensionality in different ways for growth success.

Keywords Alternative phenotypes · Functional traits · Growth · Seedlings · Tropical forest

Introduction

Ecologists have long investigated, and struggled to explain, the mechanisms that maintain species diversity (Hutchinson 1961; Clark 2010). Diversity patterns are driven by differential demographic outcomes, which arise from how phenotypes interact with the environment (Ackerly 2003; HilleRisLambers et al. 2012). Relationships between phenotypes, the environment, and demographic outcomes are complex, but high-dimensional trait-based trade-offs have been hypothesized as being important for maintaining species and functional diversity in communities (Clark et al. 2010; Adler et al. 2013; Kraft et al. 2015; D'Andrea and Ostling 2016). While these relationships have been investigated at the community level, the presence of these complex relationships within species has gone largely unconsidered in trait-based ecology, despite the known importance of intraspecific variation for generating and maintaining species diversity (Hart et al. 2016; Turcotte and Levine 2016).

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One way ecologists have examined the relationships between phenotypes, the environment, and demographic rates is by investigating the presence of alternative phenotypes, defined as combinations of different phenotypic traits leading to similar demographic success in a given environment (Marks and Lechowicz 2006; Laughlin and Messier 2015; Dwyer and Laughlin 2017; Laughlin et al. 2018). In more general terms, phenotypically dissimilar individuals of the same species, those with different functional forms, can have similar performance in the same environment (Marks 2007; Dias et al. 2019; Nolting and Holsinger 2022). Alternative phenotypes arise when the relationship between a trait and performance is dependent on an interaction with another trait (Marks and Lechowicz 2006; Worthy et al. 2020). Evidence is mounting for the presence of alternative phenotypes among species (Pistón et al. 2019; Worthy et al. 2020; Umana et al. 2021a, b; Nolting and Holsinger 2022) but lacking are empirical tests of their presence within species.

A major theme from previous work is that although there is evidence of multiple alternative phenotypes among species in communities leading to demographic success, the number of different trait combinations is relatively small compared to the number of species in the study systems (Dias et al. 2019; Pistón et al. 2019; Worthy et al. 2020; Li et al. 2021). For example, Worthy et al. (2020) found evidence of only 8 different alternative phenotypes in a community composed of 122 species. To reconcile the low number of alternative phenotypes found among species in communities with high levels of species diversity, one may assume that multiple species within the community share the same functional forms. According to this hypothesis, some species would have highly variable traits allowing individuals within the species to have alternative phenotypes that overlap with those of other species in the community. The alternative to this hypothesis would be that some species do not have intraspecific alternative phenotypes where individuals within the species have similar functional forms.

Evidence of intraspecific alternative phenotypes, would however, call into question how high species diversity can be maintained in communities. If individuals within species have different functional forms for acquiring resources and achieving demographic success, intraspecific competition could be weaker than interspecific competition, altering coexistence dynamics (Lotka 1925; Volterra 1926; MacArthur and Levins 1964; Levin 1970; Tilman 1988; Chesson 2000). Though, as highlighted above, prior research suggests that multiple species share the same intraspecific alternative phenotypes with individuals of multiple species having the same set of functional forms (Laughlin et al. 2018; Pistón et al. 2019; Worthy et al. 2020; Li et al. 2021). In this scenario, interspecific competition for resources would be high and the maintenance of species diversity in communities would likely only be possible if species are temporally or spatially segregating the environment. Species could benefit from temporal segregation through the storage effect, where species with the same functional forms are favored at different time periods (Chesson and Warner 1981; Chesson 2000; Adler et al. 2013). Species could also spatially segregate to reduce competition when they have the same functional forms (Chesson 2000; Wright 2002), which may be evident in co-occurrence patterns of species. Of course, there could be a combination of all of these possibilities at work.

In this research, we aimed to (1) determine the presence or absence of intraspecific alternative phenotypes, (2) investigate if different species use the same alternative phenotypes for growth success, and (3) evaluate how these findings align with species co-occurrence patterns. By answering these questions, we can gain an understanding of the high-dimensional axes of trait and environmental variation along which species acquire resources for growth, how individuals within species may capitalize on this dimensionality in different ways, and the implications of these dynamics for species co-occurrence patterns in a tropical forest community.

Materials and methods

Study site

The data set used in this study comes from a tropical forest community in Xishuangbanna, in the Yunnan province of China (101°34′E, 21°36′N). The climate for this area is monsoonal with two seasons, the dry season that spans November to April and the wet season that spans May to October (Cao et al. 2008). The mean annual temperature is 21.8 °C and mean annual precipitation is 1,493 mm, with 85% of the precipitation occurring during the wet season (Cao et al. 2008). In this study, we focus on seedlings because gaining understanding of their demographic success is critical for understanding later-stage patterns of forest structure and dynamics (Green et al. 2014; Chang-Yang et al. 2021).

Seedling plot establishment and monitoring

A total of 218, 1×1 m^2, seedling plots were installed across an approximate area of 2-ha where all seedlings with a height of less than or equal to 50 cm were tagged and identified. Height of these seedlings was taken during the installation of the plots and at the end of a yearlong census from 2013 to 2014. Surviving seedlings were then harvested for functional trait quantification.

Species data set

Most species in this community were rare, with few common species. Since this study focuses on variation within species, many species were eliminated from analyses due to lack of abundance. There were 122 species total among the plots, but this study includes the 3 species with at least 100 individuals, each from a different genus and family (Table S1). *Pseuduvaria indochinensis* (Annonaceae) is a canopy tree species reaching 20 m in height as an adult and based on importance value index, is one of the most important species in the forested region of south-west China (Lü et al. 2010). However, the canopy of this forest community is dominated by the slow growing, emergent species *Parashorea chinensis* (Dipterocarpaceae) while the evergreen shrub, *Pittosporopsis kerrii* (Icacinaceae), dominates the understory (Cao et al. 2008).

Functional traits

Two functional trait measurements were taken on each harvested seedling—one organ-level trait, leaf mass per unit area (LMA), and one biomass allocation trait, root mass fraction (RMF). LMA was quantified by first measuring the fresh leaf area of one to three fully expanded leaves for each individual, and then dividing this value by the dry mass of the leaves. Leaves and roots were manually separated in the lab and dried in the oven for 72 h at 70 °C. RMF was quantified as the total root dry mass divided by the total plant dry mass as previously reported in Umaña et al. (2015). Trait variables were natural log-transformed and scaled to a mean of zero for each species separately prior to analyses (Table S1).

These two traits (LMA and RMF) were specifically chosen for measurement as they represent major allocation trade-offs at both the organ and whole plant levels that should impact growth success (Poorter et al. 2012). LMA represents the leaf economics spectrum (Reich et al. 1997; Wright et al. 2004) where individuals with higher LMA have lower mass-based photosynthetic rates and longer leaf lifespans but individuals with lower LMA have higher mass-based photosynthetic rates and shorter leaf life spans. RMF is often measured to quantify allocation to non-photosynthetic tissues, belowground biomass allocation, and serves as an indicator of root function (Freschet et al. 2021a) where higher RMF would be expected when belowground resources are limited to increase exploitation of the soil (Freschet et al. 2021b). Previous work has indicated that both of these traits are highly responsive to light gradients and soil nutrients, making them of particular interest (Freschet et al. 2015). Further, studies have shown that individuals differentially allocate biomass aboveground and belowground, relying on different plant organs, leaves versus roots, and using different strategies to acquire resources for growth (Worthy et al. 2020; Umaña et al. 2021a, b).

Quantifying growth rates

To determine the relative growth rate (RGR) of each individual, the change in log-transformed height was calculated as:

$$\mathrm{RGR} = \left(\log\left(M_{t+\Delta t}\right) - \log\left(M_t\right)\right)/\Delta t$$

The variable M_t is the height at successive time steps t (Hoffmann and Poorter 2002). A value of 1 was added to all observed RGR values and the data were then natural log-transformed and scaled to a mean of 0 to approximate normality for each species separately. Relative growth rate served as the demographic rate of interest in this study.

Environmental variables

Light availability and soil nutrients were measured once for each plot (Table S2). Light availability was measured as the percent canopy openness determined using photographs taken with a Nikon FC-E8 lens and a Nikon Coolpix 4500 camera 1 m above the ground over each plot before sunrise with cloudy conditions. Images were analyzed using Gap Light Analyser software (http://www.caryinstitute.org/science-program/our-scientists/dr-charles-d-canham/gap-light-analyzer-gla). To measure soil nutrient levels, 50 g of the topsoil (0–10 cm in depth) was collected from each corner of each plot. Samples were air dried and sifted before analyses. Cation availability was determined using the Mehlich III extraction method and atomic emission inductively coupled plasma spectrometry (AE-ICP). Total nitrogen and carbon content were determined by total combustion using an auto-analyzer and pH measured with a pH meter. All soil analyses were conducted at the Biogeochemical Laboratory at Xishuangbanna Tropical Botanical Garden.

The environmental variables were natural log-transformed and scaled to a mean of zero before analyses. Soil nutrients were condensed into principal components and the first two orthogonal axes were used in analyses with 39% of the variation explained by the first axis and 21% of the variation explained by the second axis (Table S3). PC1 scores were negatively associated with K, Mg, and Zn and PC2 scores were negatively associated with Ca and P (Fig. S1).

Linear mixed-effects model description

We built linear mixed-effects models using a Bayesian approach for each species separately to evaluate relationships between traits, the environment, and relative growth rate. Variables were chosen for inclusion in the model based on prior evidence of their significant effects on growth performance (Baraloto et al. 2006; Poorter et al. 2012; Reich 2014; Umaña et al. 2018; Worthy et al. 2020). For each species' model, RGR followed a log-normal distribution:

$$\log\mathrm{RGR_i} \sim N(z_i, \sigma_z),$$

where z_i was the relative growth rate of each individual and σ_z was the variance. The general formula of the model was:

$$\begin{aligned} z_i = {} & \alpha_p + \beta_1\mathrm{LMA} + \beta_2\mathrm{RMF} + \beta_3\mathrm{InitialSize} + \beta_4\mathrm{Light} \\ & + \beta_5\mathrm{Soil1} + \beta_6\mathrm{Soil2} + \beta_7\mathrm{LMA}\times\mathrm{RMF} + \beta_8\mathrm{LMA}\times\mathrm{Light} \\ & + \beta_9\mathrm{LMA}\times\mathrm{Soil1} + \beta_{10}\mathrm{LMA}\times\mathrm{Soil2} + \beta_{11}\mathrm{RMF}\times\mathrm{Light} \\ & + \beta_{12}\mathrm{RMF}\times\mathrm{Soil1} + \beta_{13}\mathrm{RMF}\times\mathrm{Soil2} + \beta_{14}\mathrm{LMA} \\ & \times\mathrm{RMF}\times\mathrm{Light} + \beta_{15}\mathrm{LMA}\times\mathrm{RMF}\times\mathrm{Soil1} \\ & + \beta_{16}\mathrm{LMA}\times\mathrm{RMF}\times\mathrm{Soil2}, \end{aligned}$$

where z_i was the relative growth rate of each individual and α_p was a random effect for plot.

The plot random effect was given a diffuse normal prior for mean and a diffuse half-Cauchy prior for variance, which is useful because it is a thick-tailed probability distribution that is weakly regularizing (McElreath 2016). All other variables were given diffuse normal priors. All models were fit using Hamiltonian Monte Carlo sampling implemented in Stan (Stan Development Team 2020) interfaced with R programming language (R Development Core Team 2016) using the *rethinking* (McElreath 2016) and *rstan* (Stan Development Team 2020) packages. We ran 4 independent chains with random initial values for 50,000 iterations and a warm-up period of 5,000 iterations. Parameter estimates and 95% credible intervals were obtained from the posterior distributions. Convergence of the chains along with each variable in the models was assessed visually and using the Gelman-Rubin convergence diagnostic with a cutoff value of 1.1 (Gelman and Rubin 1992). A parameter was considered significant if its 95% credible interval did not overlap zero.

Assessing intraspecific alternative phenotypes

To determine the presence of alternative phenotypes within a species, two conditions had to be supported. First, the two-way interaction term between LMA and RMF or any three-way interaction term, between the two traits and an environmental variable, in the model had to be significant with 95% credible intervals around the parameter estimate not overlapping zero. Second, the first partial derivative of the fitted model had to switch signs showing that the slope of the relationship between RGR and a trait linearly depended on another trait and/or the environment (Laughlin et al. 2018). The first partial derivative with respect to LMA for the LMA × RMF interaction was calculated as:

$$\frac{\partial\mathrm{RGR}}{\partial\mathrm{LMA}} = \beta_1 + \beta_7 \times \mathrm{RMF},$$

where β_1 and β_7 are estimated coefficients from the fitted models with β_7 multiplied by observed values of RMF. A similar methodology was used to calculate the first partial derivative of the three-way interactions. As an example, the first partial derivative of the interaction LMA × RMF × light was calculated as:

$$\frac{\partial\mathrm{RGR}}{\partial\mathrm{LMA}} = \beta_1 + (\beta_7 \times \mathrm{RMF}) + (\beta_8 \times \mathrm{Light}) + ((\beta_{14} \times (\mathrm{RMF} \times \mathrm{Light})),$$

where β_1, β_7, β_8, and β_{14} are estimated coefficients from the fitted models with β_7 multiplied by observed values of RMF, β_8 multiplied by observed values of light, and β_{14} multiplied by observed values of both RMF and light. Calculated values were then plotted to determine if the relationship between LMA and RGR switched signs across the range of RMF and/or the environmental variable in the interaction term (Laughlin et al. 2018; Worthy et al. 2020). A switch in sign indicates that the derivative passes through zero creating a "saddle" at intermediate trait values or environmental conditions due to the probability surface being pulled downward (Laughlin et al. 2018). Hence, the slope can be negative at one end of the gradient and positive at the other or vice versa (Laughlin et al. 2018).

Quantifying contribution of variables to RGR

We determined the contribution of each model variable to RGR for each species by multiplying the partial regression coefficient, separately, by the mean, minimum, and maximum observed trait and/or environmental variable following Arnold (1983). This allowed us to determine for each species which model variable contributed most positively to RGR and more specifically, the importance of intraspecific alternative phenotypes to RGR. The two principal component axes of the soil variables included negative values, so the exponentials of these values were used to eliminate the negative values so that the contribution of these variables could be calculated.

Co-occurrence patterns

Co-occurrence patterns of the species were determined using the *cooccur* package (Griffith et al. 2016) in R based on the presence or absence of species across the seedling plots. This function calculated the observed and expected frequencies of co-occurrence between each pair of species, with the expected frequency based on the distribution of each species being random and independent of the other species (Veech 2013). The function returned the probability of co-occurrence for all pairs of species along with pairs that have a higher or lower value of co-occurrence than could have been obtained by chance.

Results

Assessing intraspecific alternative phenotypes

Each species' model was assessed for the presence of intraspecific alternative phenotypes (Table S4). Two of the three species showed evidence of alternative phenotypes with significant interactions found between the two traits (LMA and RMF) and between the two traits and an environmental variable (Fig. 1). *P. indochinensis* did not show evidence of intraspecific alternative phenotypes but did have two significant two-way interactions between LMA and soil component 1 and the between RMF and light (Fig. S2). *P. chinensis* and *P. kerrii* both showed evidence of intraspecific alternative phenotypes, each having a significant two-way interaction between LMA and RMF (Fig. 2). For both species, RGR was higher when individuals had high LMA and low RMF or when individuals had low LMA and high RMF (Fig. 2). A significant three-way interaction was also found between the two traits and a component of soil nutrients in models of both of these species. *P. chinensis* had a significant three-way interaction between LMA, RMF, and soil component 2 (Fig. 3A). At the poor nutrient end of the soil nutrient gradient, individuals had higher RGR when they combined low LMA with low RMF (Fig. 3A). At the high nutrient end of the soil variable, there were two peaks in RGR, one for individuals with high LMA and low RMF and one for individuals with low LMA and high RMF (Fig. 3A). *P. kerrii* had a significant three-way interaction between LMA, RMF, and soil component 1 (Fig. 3B). At the low nutrient end of the soil gradient, individuals had higher RGR when they combined high LMA with high RMF or low LMA with low RMF (Fig. 3B). At the opposite end of the soil gradient with high nutrients, there were also two peaks in RGR, one for individuals with high LMA and low RMF and one for individuals with low LMA and high RMF (Fig. 3B).

Quantifying contribution of variables to RGR

The contribution of each model variable to RGR of each species was calculated at the mean, minimum, and maximum observed values of each variable (Table 1). Of the two traits in the models, LMA had a larger, direct contribution to RGR than RMF for all species when not considering how the traits are influenced by environmental variables or each other (Table 1). For two species, minimum LMA contributed most where for *P. kerrii* maximum

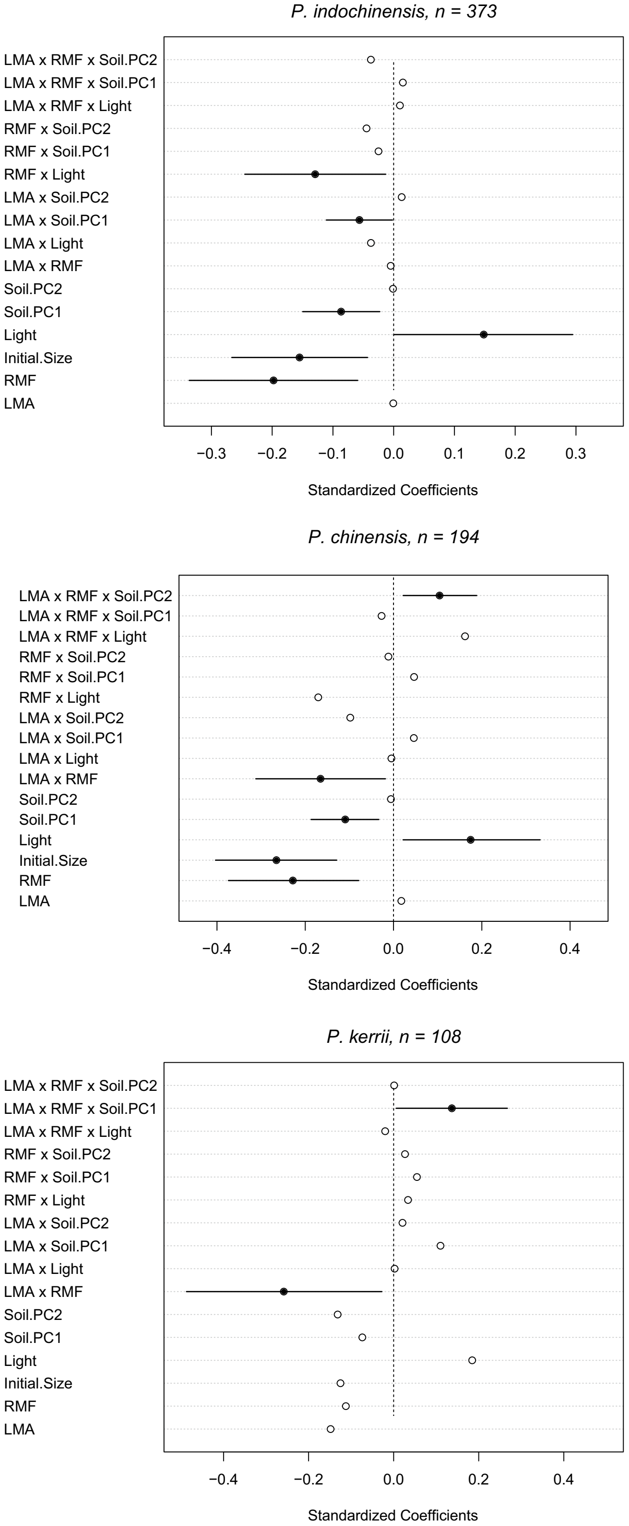

Fig. 1 Standardized regression coefficients for each of the three species in the study for models examining the relationships between traits, environmental variables, and their interactions on seedling relative growth rate. Circles represent posterior mean values and filled circles indicate significant effects. Lines representing 95% credible intervals are only presented for significant effects to minimize the *x* axis and allow better viewing. All variables were natural log-transformed and scaled to unit variance. PC1 scores are negatively associated with K, Mg, and Zn and PC2 scores are negatively associated with Ca and P

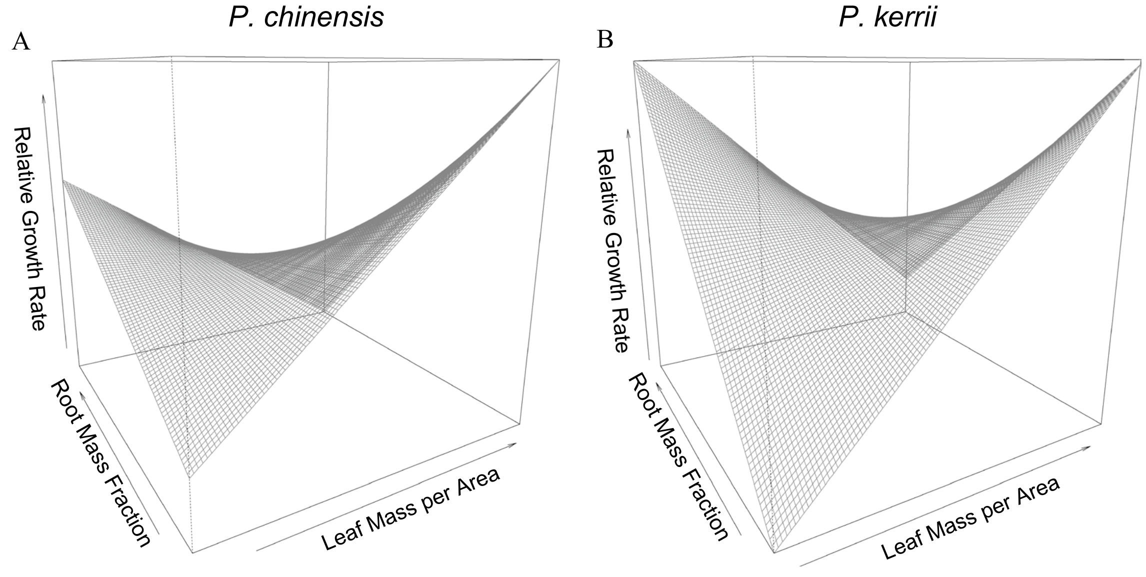

Fig. 2 *P. chinensis* and *P. kerrii* each had a significant two-way interaction between leaf mass per area (LMA) and root mass fraction (RMF) showing evidence of intraspecific alternative phenotypes. For both species, *P. chinensis* (**A**) and *P. kerrii* (**B**) individuals had higher relative growth rate (RGR) when they had high LMA and low RMF, but also had higher RGR when they combined low LMA with high RMF

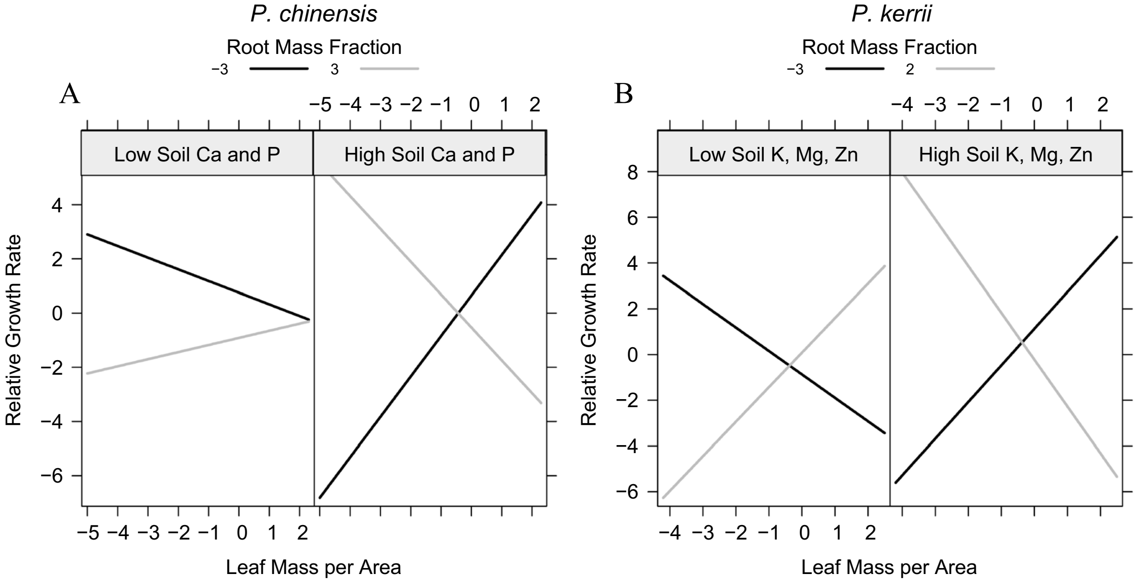

Fig. 3 *P. chinensis* and *P. kerrii* each had a significant three-way interaction between leaf mass per area (LMA), root mass fraction (RMF), and one of the soil nutrient principal components. **A** For *P. chinensis*, the interaction was between LMA, RMF, and soil component 2. Soil component 2 is negatively associated with Ca and P. At the low nutrient end of the soil gradient, individuals had higher relative growth rate (RGR) when they combined low LMA with low RMF. At the high nutrient end of the soil gradient, there were two peaks in RGR, one for individuals that combined high LMA with low RMF and one for individuals that combined low LMA with high RMF. **B** For *P. kerrii*, the interaction was between LMA, RMF, and soil component 1. Soil component 1 is negatively associated with Mg, K, and Zn. At the low end of the soil gradient, individuals had higher RGR when they combined high LMA with high RMF or low LMA with low RMF. At the opposite end of the gradient with high soil nutrients, there were two peaks in RGR, one for individuals with high LMA and low RMF and one for individuals with low LMA and high RMF. All variables were scaled and natural log-transformed

Table 1 The contribution of each model variable to relative growth rate (RGR) was calculated for each species by multiplying its partial regression coefficient, separately, by the mean, minimum (min), and maximum (max) observed trait and/or environmental variable

Species	Largest trait contribution	Largest environmental contribution	Largest overall contribution
Pittosporopsis kerrii	Max LMA	Max light	Max RMF:Soil.PC2
Parashorea chinensis	Min LMA	Max light	Max RMF:Soil.PC2
Pseuduvaria indochinensis	Min LMA	Max light	Max light

The largest positive contributor to growth was determined among the traits (largest trait contribution), among the environmental variables (largest environmental contribution), and among all model variables (largest overall contribution)

LMA contributed most to RGR (Table 1). For the environmental variables, maximum observed light was the largest contributor to RGR for all species (Table 1). Despite finding evidence of intraspecific alternative phenotypes for *P. chinensis* and *P. kerrii*, these variables did not contribute most to RGR in these species. The overall largest, positive contributor to RGR for these two species was the interaction between maximum RMF and maximum soil component 2, high Ca and P in the soil (Table 1). For *P. indochinensis*, maximum light was the largest contributing variable to RGR (Table 1).

Comparisons and drivers of species alternative phenotypes

One species in this study, *P. indochinensis,* did not show evidence of intraspecific alternative phenotypes. However, significant interactions were found for this species between singular traits and environmental variables (Fig. S2). The two other species in this study did show evidence of intraspecific alternative phenotypes (Figs. 1, 2, 3). *P. kerrii* and *P. chinensis* share one interaction term with evidence of multiple intraspecific functional forms, LMA × RMF (Fig. 2), and combine these traits in the same two ways to achieve similar RGR in high soil nutrient environments (Fig. 3). However, in poor soil nutrient environments, individuals within these species use different strategies to achieve higher RGR, where *P. kerrii* individuals maintain two functional forms (i.e., intraspecific alternative phenotypes), but *P. chinensis* individuals only achieve higher RGR by combining low LMA with low RMF (Fig. 3). Interestingly, all three species significantly, negatively co-occur on the landscape (Table S5), suggestive of species spatially segregating the environment due to similarity in functional forms used to acquire resources.

While there was variation among species in the presence and type of functional forms, all species were similar in what variables contributed most to increased RGR (Table 1). LMA dominated as a singular trait, but RMF was more common as part of interaction terms for the largest overall contributing variable to increased RGR (Table 1). All three species had the same environmental variable with the highest contribution, maximum light, and two of the species had the same variable with the largest overall contribution to RGR, maximum RMF interacting with maximum soil component 2 (Table 1). Similarity between all species for which variables contributed most to increased RGR could suggest an underlying best strategy for growth, higher RMF in low Ca and P soils, among these abundant seedling species. However, other significant variables indicate these species capitalize on differentiation along other trait and environmental axes and/or use intraspecific alternative phenotypes to acquire resources for growth. Combined, this suggests that light and soil nutrients may be the most limiting factors for these species in this environment, so it is always better to capture more of them.

Discussion

In this study, we have shown that two of the three most abundant seedling species in a tropical forest community have intraspecific alternative phenotypes that contribute to both similarities and differences in how these species achieve growth success. Below we discuss how variability among species in the presence, type, and importance of intraspecific alternative phenotypes interacts with the environment to drive species-specific strategies for growth.

Two of the three species in this study showed evidence of intraspecific alternative phenotypes. Specifically, individuals within these species had different trait × trait and trait × trait × environment combinations that led to higher RGR (Figs. 1–3). Individuals within both *P. chinensis* and *P. kerrii* combined LMA and RMF in the same two ways to achieve higher RGR overall (Fig. 2), as well as in high soil nutrient environments (Fig. 3). These findings support our hypothesis that multiple species may have the same intraspecific alternative phenotypes, with individuals within the different species taking the same functional forms. We also found support for these species spatially segregating the environment, with all species negatively co-occurring with the other species in the study (Table S5). Similar results have been recently reported by Xia et al. (2019) who found significant spatial niche differentiation between *P. kerrii* and *P. chinensis*, with each species occupying patches of different soil nutrients. In addition to similar intraspecific alternative phenotypes, all species in the study were similar in what variables contributed most to increased RGR (Table 1). This could suggest an underlying best strategy for growth which species deviate from to acquire limiting resources and decrease interspecific competition.

One way species may differentiate their strategies for growth in this community is by altering how they combine traits along soil nutrient gradients. Interestingly, the two species with intraspecific alternative phenotypes combined RMF and LMA in different ways when moving from high to low soil nutrients (Fig. 3), *P. kerrii* switching to two different successful functional forms and *P. chinensis* individuals converging to one strategy for success. This allows individuals within these species to change or combine resource acquisition strategies (acquisitive and conservative) within and among environments along soil nutrient gradients to achieve growth success (Fig. 3). Previous studies have suggested that high trait variability within species could allow them to maintain dominance in communities which seems plausible here as these species are some of the most abundant in this community (Richards et al. 2006; Hart et al. 2016; Pérez-Ramos et al. 2019). However, we note that this study includes only three species that are the most abundant in the seedling community and that we did not investigate moderately abundant or rare species due to sample size issues. Importantly, however, our results highlight that individuals within species are highly variable, with very phenotypically different individuals having similar growth performance within the same environment, suggesting that using species mean traits to estimate individual growth or species mean growth may have critical conceptual and empirical consequences (Yang et al. 2018, 2020; Swenson et al. 2020).

The species in this study showed evidence of species-specific strategies for growth across multiple axes of trait and environmental variation. Commonly, we found that interactions between traits and the environment contributed most to species' RGR, such that similarity in how species acquire resources for growth may depend on which end of the environmental gradient the species is located in the community. A major takeaway from previous work was the suggestion that there are only a few dimensions along which species compete where they can partition resources and decrease interspecific competition (Clark et al. 2004, 2007; Condit et al. 2006; Mohan et al. 2007; Clark 2010). This dynamic has been discussed previously as the paradox of low diversity where models tend to find low levels of species diversity, which do not align with observed levels, and are unable to explain how so many species can inhabit communities (Hutchinson 1961; Clark 2010). Our dataset size limits application of our findings to understanding how high species diversity can be maintained in communities. However, our findings and others (D'Andrea et al. 2018) do highlight the large amount and multi-dimensional nature of species differences in how they combine traits and alter trait combinations along environmental gradients to acquire resources for growth which deserves further investigation.

Overall, our results suggest that these common species acquire resources for growth along multiple as well as high-dimensional axes of trait and environmental variation. Our findings stress that individuals within species are able to exploit this multi-dimensionality in different ways, which would have gone unobserved in species-level analyses (Clark 2010). While observational, this study considers multiple environmental variables, common functional traits, and their interactions to capture a broad range of ecological dimensions used to distinguish how species acquire resources for growth and understand similarities and differences in resource acquisition strategies among species.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-024-05553-8.

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Code availability Code for the analyses in this manuscript is available at https://zenodo.org/doi/10.5281/zenodo.11005323.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Ackerly DD (2003) Community assembly, niche conservatism, and adaptive evolution in changing environments. Int J Plant Sc 164:S165–S184. https://doi.org/10.1086/368401

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJB (2013) Trait-based tests of coexistence mechanism. Ecol Lett 16:1294–1306. https://doi.org/10.1111/ele.12157

Arnold SJ (1983) Morphology, performance and fitness. Am Zool 23:347–361. https://doi.org/10.1093/icb/23.2.347

Baraloto C, Bonal D, Goldberg DE (2006) Differential seedling growth response to soil resource availability among nine neotropical tree species. J Trop Ecol 22:487–497. https://doi.org/10.1017/S0266467406003439

Cao M, Zhu H, Wang H, Lan G, Hu Y, Zhou S, Deng X, Cui J (2008) Xishuangbanna tropical seasonal rainforest dynamics plot: tree distribution maps, diameter tables and species documentation. Yunnan Science and Technology Press, Kunming

Chang-Yang C-H, Needham J, Lu C-L, Hsieh C-F, Sun I-F, McMahon SM (2021) Closing the life cycle of forest trees: the difficult dynamics of seedling-to-sapling transitions in a subtropical rainforest. J Ecol 109:2705–2716. https://doi.org/10.1111/1365-2745.13677

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chesson PL, Warner RR (1981) Environmental variability promotes coexistence in lottery competitive systems. Am Nat 117:923–943. https://doi.org/10.1086/283778

Clark JS (2010) Individuals and the variation needed for high species diversity in forest trees. Science 327:1129–1132. https://doi.org/10.1126/science.1183506

Clark JS, LaDeau S, Ibanez I (2004) Fecundity of trees and the colonization-competition hypothesis. Ecol Monogr 74:415–442. https://doi.org/10.1890/02-4093

Clark JS, Dietze M, Chakraborty S, Agarwal PK, Ibanez I, LaDeau S, Wolosin M (2007) Resolving the biodiversity paradox. Ecol Lett 10:647–662. https://doi.org/10.1111/j.1461-0248.2007.01041.x

Clark JS, Bell D, Chu C, Courbaud B, Dietze M, Hersh M, HilleRisLambers J, Ibášez I, LaDeau S, McMahon S, Metcalf J, Mohan J, Moran E, Pangle L, Pearson S, Salk C, Shen Z, Valle D, Wyckoff P (2010) High-dimensional coexistence based on individual variation: a synthesis of evidence. Ecol Monogr 80:569–608. https://doi.org/10.1890/09-1541.1

Condit R, Ashton P, Bunyavejcheqin S, Dattaraja HS, Davies S, Esufali S, Ewango C, Foster R, Gunatilleke IAUN, Gunatilleke CVS, Hall P, Harms KE, Hart T, Hernandez C, Hubbell S, Itoh A, Kiratiprayoon S, LaFrankie J, Loo de Lao S, Makana J-R, Noor Md NS, Kassim AR, Russo S, Sukumar R, Samper C, Suresh HS, Tan S, Thomas S, Valencia R, Vallejo M, Villa G, Zillio T (2006) The importance of demographic niches to tree diversity. Science 313:98–101. https://doi.org/10.1126/science.1124712

D'Andrea R, Ostling A (2016) Challenges in linking trait patterns to niche differentiation. Oikos 125:139–1385. https://doi.org/10.1111/oik.02979

D'Andrea R, Ostling A, O'Dwyer JP (2018) Translucent windows: how uncertainty in competitive interactions impacts detection of community pattern. Ecol Lett 21:826–835. https://doi.org/10.1111/ele.12946

Dias ATC, Rosado BHP, de Bello F, Pistón N, de Mattos EA (2019) Alternative plant designs: consequences for community assembly and ecosystem functioning. Ann Bot 125:391–398. https://doi.org/10.1093/aob/mcz180

Dwyer JM, Laughlin DC (2017) Constraints on trait combinations explain climatic drivers of biodiversity: the importance of trait covariance in community assembly. Ecol Lett 20:872–882. https://doi.org/10.1111/ele.12781

Freschet GT, Swart EM, Cornelissen JHC (2015) Integrated plant phenotypic response to contrasting above- and below-ground resources: key roles of specific leaf area and root mass fraction. New Phytol 206:1247–1260. https://doi.org/10.1111/nph.13352

Freschet GT, Pagès L, Iversen CM, Comas LH, Rewald B, Roumet C, Klimešová J, Zadworny M, Poorter H, Postma JA, Adams TS, Bagniewska-Zadworna A, Bengough AG, Blancaflor EB, Brunner I, Cornelissen JHC, Garnier E, Gessler A, Hobbie SE, Meier IC, Mommer L, Picon-Cochard C, Rose L, Ryser P, Scherer-Lorenzen M, Soudzilovskaia NA, Stokes A, Sun T, Valverde-Barrantes OJ, Weemstra M, Weigelt A, Wurzburger N, York LM, Betterman SA, Gomes de Moraes M, Janeček Š, Lambers H, Salmon V, Tharayil N, McCormack ML (2021a) A starting guide to root ecology: strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements. New Phytol 232:973–1122. https://doi.org/10.1111/nph.17572

Freschet GT, Roumet C, Comas LH, Weemstra M, Bengough AG, Rewald B, Bardgett RD, De Deyn GB, Johnson D, Klimešová J, Lukac M, McCormack ML, Meier IC, Pagès L, Poorter H, Prieto I, Wurzburger N, Zadworny M, Bagniewska-Zadworna A, Blancaflor EB, Brunner I, Gessler A, Hobbie SE, Iversen CM, Mommer L, Picon-Cochard C, Postma JA, Rose L, Ryser P, Scherer-Lorenzen M, Soudzilovskaia NA, Sun T, Valverde-Barrantes OJ, Weigelt A, York LM, Stokes A (2021b) Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. New Phytol 232:1123–1158. https://doi.org/10.1111/nph.17072

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Stat Sci 7:457–511. https://doi.org/10.1214/ss/1177011136

Green PT, Harms KE, Connell JH (2014) Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. P Natl Acad Sci USA 111:18649–18654. https://doi.org/10.1073/pnas.1321892112

Griffith DM, Veech JA, Marsh CJ (2016) Cooccur: Probabilistic species co-occurrence analysis in R. J Stat Softw 69:1–17. https://doi.org/10.18637/jss.v069.c02

Hart SP, Schreiber SJ, Levine JM (2016) How variation between individuals affects species coexistence. Ecol Lett 19:825–838. https://doi.org/10.1111/ele.12618

HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. Annu Rev Ecol Evol S 43:227–248. https://doi.org/10.1146/annurev-ecolsys-110411-160411

Hoffmann WA, Poorter H (2002) Avoiding bias in calculations of relative growth rate. Ann Bot 80:37–42. https://doi.org/10.1093/aob/mcf140

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95(1):37–145. https://doi.org/10.1086/282171

Kraft NJB, Godoy O, Levine JM (2015) Plant functional traits and the multidimensional nature of species coexistence. P Natl Acad Sci USA 112:797–802. https://doi.org/10.1073/pnas.1413650112

Laughlin DC, Messier J (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. Trends Ecol Evol 30:487–496. https://doi.org/10.1016/j.tree.2015.06.003

Laughlin DC, Strahan RT, Adler PB, Moore MM (2018) Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. Ecol Lett 21:411–421. https://doi.org/10.1111/ele.12914

Levin SA (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. Am Nat 104:413–423

Li Y, Jiang Y, Shipley B, Li B, Luo W, Chen Y, Zhao K, He D, Rodríguez-Hernández DI, Chu C (2021) The complexity of trait-environment performance landscapes in a local subtropical forest. New Phytol 229:1388–1397. https://doi.org/10.1111/nph.16955

Lotka AJ (1925) Elements of physical biology. Williams and Wilkins, Baltimore, MD

Lü XT, Yin JX, Tang JW (2010) Structure, tree species diversity and composition of tropical seasonal rainforests in Xishuangbanna, South-West China. J Trop Forest Sci 22:260–270

MacArthur RH, Levins R (1964) Competition, habitat selection, and character displacement in a patchy environment. P Natl Acad Sci USA 51:1207–1210

Marks CO (2007) The causes of variation in tree seedling traits: the roles of environmental selection versus change. Evolution 61:455–469. https://doi.org/10.1111/j.1742-4658.2007.00021.x

Marks CO, Lechowicz MJ (2006) Alternative designs and the evolution of functional diversity. Am Nat 167:55–66. https://doi.org/10.1086/498276

McElreath R (2016) Statistical rethinking: a bayesian course with examples in R and stan. Chapman & Hall/CRC, Boca Raton

Mohan JE, Clark JS, Schlesinger WH (2007) Long-term CO_2 enrichment of a forest ecosystem: implications for forest regeneration and success. Ecol Appl 17:1198–1212. https://doi.org/10.1890/05-1690

Nolting KM, Holsinger KE (2022) Alternative designs lead to similar performance when traits and performance vary on different axes. bioRxiv. https://doi.org/10.1101/2022.10.05.511045

Pérez-Ramos IM, Matías L, Gómez-Aparicio L, Godoy Ó (2019) Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. Nat Commun 10:2555. https://doi.org/10.1038/s41467-019-10453-0

Pistón N, de Bello F, Dias ATC, Götzenberger L, Rosado BHP, de Mattos EA, Salguero-Gómez R, Carmona CP (2019) Multidimensional ecological analyses demonstrate how interactions between functional traits shape fitness and life history strategies. J Ecol 107:2317–2328. https://doi.org/10.1111/1365-2745.13190

Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. New Phytol 193:30–50. https://doi.org/10.1111/j.1469-8137.2011.03952.x

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reich PB (2014) The world-wide "fast-slow" plant economics spectrum: a traits manifesto. J Ecol 102:275–301. https://doi.org/10.1111/1365-2745.12211

Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci USA 94:13730–13734. https://doi.org/10.1073/pnas.94.25.13730

Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. Ecol Lett 9:981–993. https://doi.org/10.1111/j.1461-0248.2006.00950.x

Stan Development Team (2020) RStan: the R interface to Stan. R package version 2.19.3. http://mc-stan.org

Swenson NG, Worthy SJ, Eubanks D, Iida Y, Monks L, Petprakob K, Rubio VE, Staiger K, Zambrano J (2020) A reframing of trait-demographic rate analyses for ecology and evolutionary biology. Int J Plant Sci 181:33–43. https://doi.org/10.1086/706189

Tilman D (1988) Dynamics and structure of plant communities. Monographs in population biology 26. Princeton University Press, Princeton

Turcotte MM, Levine JM (2016) Phenotypic plasticity and species coexistence. Trends Ecol Evol 31:803–813. https://doi.org/10.1016/j.tree.2016.07.013

Umaña MN, Zhang C, Cao M, Lin L, Swenson NG (2015) Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. Ecol Lett 18:1329–1337. https://doi.org/10.1111/ele.12527

Umaña MN, Zipkin EF, Zhang C, Cao M, Lin L, Swenson NG (2018) Individual-level trait variation and negative density dependence affect growth in tropical tree seedlings. J Ecol 106:2446–2455. https://doi.org/10.1111/1365-2745.13001

Umaña MN, Arellano G, Swenson NG, Zambrano J (2021a) Tree seedling trait optimization and growth in response to local-scale soil and light variability. Ecology 102:e03252. https://doi.org/10.1002/ecy.3252

Umaña MN, Cao M, Lin L, Swenson NG, Zhang C (2021b) Trade-offs in above- and below-ground biomass allocation influencing seedling growth in a tropical forest. J Ecol 109:1184–1193. https://doi.org/10.1111/1365-2745.13543

Veech JA (2013) A probabilistic model for analyzing species co-occurrence. Global Ecol Biogeogr 22:252–260. https://doi.org/10.1111/j.1466-8238.2012.00789.x

Volterra V (1926) Fluctuations in the abundance of a species considered mathematically. Nature 118:558–560

Worthy SJ, Laughlin DC, Zambrano J, Umaña MN, Zhang C, Lin L, Cao M, Swenson NG (2020) Alternative designs and tropical tree seedling growth performance landscapes. Ecology 101:e03007. https://doi.org/10.1002/ecy.3007

Wright SJ (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130:1–14. https://doi.org/10.1007/s004420100809

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827. https://doi.org/10.1038/nature02403

Xia S-W, Cao M, Yang X, Chen J, Goodale UM (2019) Fine scale heterogeneity of soil properties causes seedling spatial niche separation in a tropical rainforest. Plant Soil 438:435–445. https://doi.org/10.1007/s11104-019-04027-8

Yang J, Cao M, Swenson NG (2018) Why functional traits do not predict trait demographic rates. Trends Ecol Evol 33:326–336. https://doi.org/10.1016/j.tree.2018.03.003

Yang J, Song X, Cao M, Deng X, Zhang W, Yang X, Swenson NG (2020) On the modeling of tropical tree growth: the importance of intra-specific trait variation, non-linear functions and phenotypic integration. Ann Bot 127:533–542. https://doi.org/10.1093/aob/mcaa085